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Growth of earthworms *(Allolobophora caliginosa)* fed shoots and roots of barley, meadow fescue and lucerne Studies in relation to particle size, protein, crude fiber content and toxicity

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With 4 figures

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1. Introduction

Arable fields are mainly cultivated by man but the cultivating effect of earthworms must not be underestimated. They mix soil and plant residues which is especially important in ley crops, where the soil is not cultivated annually, and in annual crops where soil tillage is minimized (Edwards & Lofty 1978; Barnes & Ellis 1979). Moreover, the pattern of residue decomposition differs if mixing is done by earthworms or by the plough (Stout 1983). Earthworms contribute to soil development and mull formation by bringing together mineral soil and plant residues. This is brought about in two ways: The anécique *Lumbricus terrestris* L. feeds on crop residues which are drawn into the burrows. The endogéic *Allolobophora caliginosa* (Sav.), the most common species in arable soil, feeds on well-decomposed detritus, i.e. dead soil fauna, microflora, roots, roothairs and other plant residues mixed with mineral soil (Piearce 1978). Both species deposit casts under as well as on the soil surface and Graff (1971) estimated that 25 % of the upper 10 cm soil layer passes through earthworms yearly. In this way the litter is gradually covered by surface-deposited casts and the plant residues are mixed with the mineral soil. Soil devoid of earthworms has a layer of undecomposed plant residues on the surface and mixing is minimal (Stout & Goh 1980, Hoogerkamp *et al.* 1983).

The amount and quality of crop residues returned to the soil is very important to earthworms in arable land (Lofs-Holmin 1983a & b). When permanent grassland is brought under cultivation, the earthworm population is often drastically reduced during succeeding years (Barnes & Ellis 1979). This may largely be an effect of the gradually decreasing organic matter content in the soil. However, it is not known what quantities are needed to support an earthworm population under different crops. Conversely, little is known about how much of the crop residues, roots and shoots, are turned over by earthworms.

In order to study the influence of different plant materials in relation to their chemical and physical composition, growth experiments were performed on juvenile *A. caliginosa*. The experimental data on earthworm growth were compared with earthworm population and plant residue data from the field. A fresh mixture of soil and lucerne was found to be highly toxic to *A. caliginosa*, and experiments were designed to determine the cause.

2. Materials and methods

2.1. Earthworms

Adult *A. caliginosa* were kept in laboratory cultures at 15 °C in a mixture of farmyard manure and loam soil. Cocoons were collected by washing the substrate through a 1 mm sieve. They were stored at 5 °C for a few weeks and were thereafter hatched at 20 °C. Newly hatched individuals, similar in mass and age, were chosen for the experiments.

2.2. Soil

The soil used in all experiments was taken from Kjettslinge the research site of the "Ecology of Arable Land" project, 40 km north of Uppsala. The soil is a loam, containing 18% clay, 33% silt, 42% fine sand and 2% sand, with 5% organic matter content and pH ranging between 6.0 and 6.6 (STEEN *et al.* 1984).

2.3. Growth on different plant materials

2.3.1. Plant materials

Lucerne (*Medicago sativa* L.), meadow fescue (*Festuca pratensis* L.) and barley (*Hordeum distichum* L.) were grown in a greenhouse. Lucerne was harvested before flowering and meadow fescue was harvested before stem elongation. Above-ground plant material of barley was harvested both as green shoots, before earing, and as dry straw, excluding the ripe ears. Roots of barley were harvested before the shoots eared. All materials were rinsed free from soil and dried at 50 °C.

The materials were ground in a plant mill and sifted through sieves of 1.0 mm (all materials) and 0.2 mm (barley). To obtain 10 mm pieces fresh barley shoots and roots were cut with scissors.

The plant materials were analysed for protein content (Kjeldahl N × 6.25) and crude fiber, since these parameters can be expected to be important for earthworms (Table 1). Crude fiber content was determined after boiling with KOH and H_2SO_4 (Anonymous 1966).

Table 1. Crude protein and crude fiber in the plant materials used in the growth experiments

Plant material	Crude protein (% of d.m.)	Crude fiber (% of d.m.)	Crude protein / Crude fiber
Barley			
green shoots	18	23	0.78
straw	7	27	0.26
roots	7	30	0.23
Meadow fescue			
shoots	14	22	0.64
roots	5	28	0.18
Lucerne			
shoots	17	19	0.89
roots	15	34	0.44

Table 2. Plan of growth experiments of juvenile *A. caliginosa* fed various plant materials mixed with soil

Plant materials	Particle size (mm)	Amount (g d.m.)
Experiment I		
Meadow fescue		
shoots	<1.0	1
roots	<1.0	1
Lucerne		
shoots	<1.0	1
roots	<1.0	1
Experiment II		
Barley		
green shoots	10.0	1
straw	0.2—1.0	2
	<0.2	2
roots	10.0	1
	0.2—1.0	2
	<0.2	2

2.3.2. *Experimental design*

Plant materials and 250 ml soil weighing approximately 250 g, were mixed in plastic pots according to the experimental plan (Table 2). Soil devoid of plant material was used as control and all treatments had 5 replicates. The water content, maintained uniform by regular watering, was 30% of dry mass. One juvenile earthworm was placed in each pot. Pots were covered by lids that had a few 1 mm holes for ventilation and were kept in the dark at 15 °C. Juveniles were weighed individually after they had been rinsed in water and gently dried on filter paper. Individual masses were followed during 160 days.

Two growth experiments were performed. Experiment I was performed on lucerne and meadow fescue with a particle size <1.0 mm and an amount of 1 g per pot. In experiment II growth on barley material was investigated. Two grams per pot of ground straw and roots with a particle size <0.2 and 0.2 to 1.0 mm were added. As 10 mm pieces of roots and green shoots were very bulky, only 1 g of this particle size-class was added per pot. In experiment II the amounts of barley material were increased because in experiment I it was found that 1 g per pot supported growth for only approximately 8 weeks.

2.4. Field sampling

2.4.1. *Earthworm populations*

Earthworms were collected from a lucerne ley in the Kjettslinge field on 12 May and 15—17 September 1981, using the formalin method (RAW 1959). Four samples of 0.5 m² were taken in each of four replicates, i.e. 16 subsamples. Earthworms were determined to species, divided into juveniles and adults and weighed alive.

2.4.2. *Soil organic matter*

The field crop was a 1-year-old lucerne ley, which had been insown in barley the previous year. The lucerne was poorly established and died back extensively during the winter of 1980—1981. A shallow rotary cultivation was performed in May and lucerne was resown. The amount of plant material on the soil surface was estimated by handsorting before rotary cultivating. The total amount of organic matter, including the new supply in the soil, was estimated by washing soil cores one month after cultivation (HANSSON & STEEN 1984).

2.5. Nitrate, nitrite and ammonium content in soil-lucerne mixture

One gram of ground lucerne shoots <1.0 mm was mixed with 250 ml soil in ten plastic pots and incubated at 15 °C. The water content was 30% of dry mass. After 12 h and 1, $1^1/_2$, 2, $2^1/_2$, 3, 4, 5, 6 and 7 days one pot was selected. Two soil samples of 20 g were taken from each pot and shaken with 100 ml 2 M KCl for 2 h. Nitrate, nitrite and ammonium were determined by flow injection analysis (GINE *et al.* 1980; RUZICKA & HANSEN 1975).

2.6. Toxicity of nitrate and nitrite

The toxicity of nitrate and nitrite to *A. caliginosa* was tested in two experiments (III and IV). $NaNO_3$ and $NaNO_2$ were added to 250 ml soil in pots so that concentrations of nitrate and nitrite became as shown in Table 3. Pure soil and soil with 1,500 ppm Na^+ (Na_2HPO_4) were used as controls. The water content was 30% of dry mass.

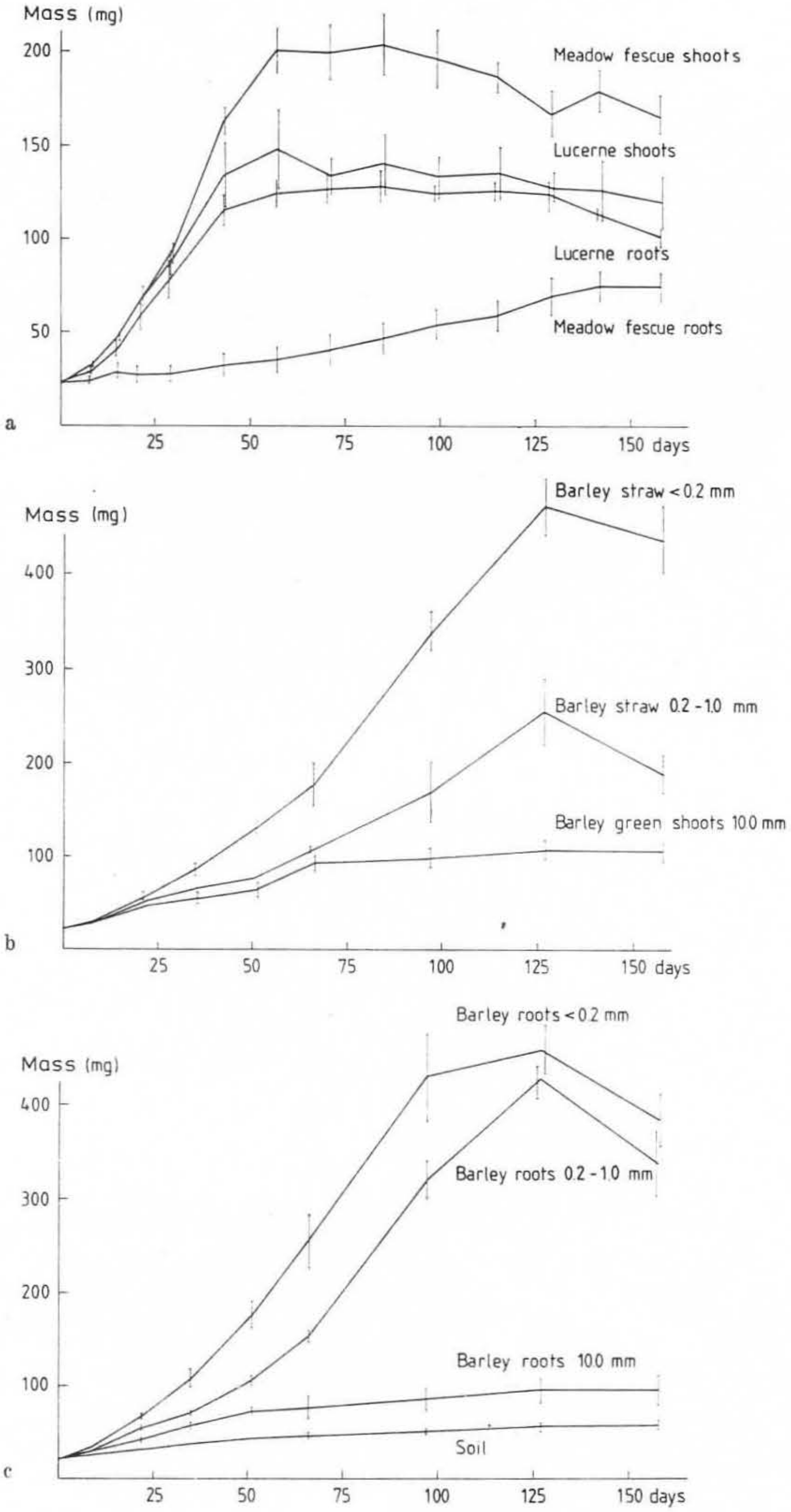
In experiment III *A. caliginosa* juveniles weighing approximately 40 mg and in experiment IV double that size were placed in pots and weighed individually every week. The pots were kept under the same conditions as in the previous experiments.

Table 3. Plan of toxicity experiments. Concentration of chemicals in soil

	Concentration (ppm)	
	Experiment III	Experiment IV
NO_3^-—N	9, 900	—
NO_2^-—N	3, 300	10, 65, 110, 225
Na^+		1,500

2.7. Calculations and statistical treatment

Maximum earthworm mass gain per g d.m. plant material was calculated for each material as maximum mass on each respective growth curve minus initial earthworm mass divided by the amount of added material. All material added was assumed to be consumed. The values were cor-


Mass (mg)
Meadow fescue shoots
Lucerne shoots
Lucerne roots
Meadow fescue roots
a
25 50 75 100 125 150 days
Barley straw < 0.2 mm
Mass (mg)
Barley straw 0.2 - 1.0 mm
Barley green shoots 10.0 mm
b
25 50 75 100 125 150 days
Barley roots < 0.2 mm
Mass (mg)
Barley roots 0.2 - 1.0 mm
Barley roots 10.0 mm
Soil
c
25 50 75 100 125 150 days

rected for the corresponding mass of earthworms at the same time in unamended soil. The growth rate (g_r) was calculated as:

$$g_r = \frac{m_2 - m_1}{t_2 - t_1}$$

where m_1 and m_2 are earthworm masses at the beginning and end of the time period ($t_2 - t_1$) respectively. To test whether growth rate was influenced by earthworm mass at the beginning of each period, "Spearman's rank correlation coefficient" was used. Analyses of variances (ANOVA) followed by the least significant difference method (LSD) were used to test differences between means.

3. Results

3.1. Growth on different plant materials

Different plant materials produced extremely different earthworm growth. Figs. 1a—c show growth curves of juvenile *A. caliginosa*. The different mass scale in Fig. 1a should be noted. No more than one of five worms was aestivating at any time, but aestivating earthworms were excluded from the calculations. In unamended soil and soil mixed with barley 10 mm or meadow fescue roots, the worm masses never reached a maximum as in other treatments. In the former materials the growth continued slowly throughout the experimental period indicating that no abrupt food shortage occurred, but the final mass gain was still comparatively small. In the other treatments maximal masses were reached after 8 weeks (1 g material) or 17 weeks (2 g material).

Table 4 shows maximum mass gain in all materials tested, irrespective of the time needed to reach this mass. Mass gain in soil devoid of plant material constituted as much as 45 to 70% of the mass gain in treatments with meadow fescue roots < 1.0 mm and barley roots or shoots 10.0 mm. The growth rate per juvenile *A. caliginosa* during the first 43 days is shown in Fig. 2. During this period the amount of plant material did not seem to influence growth. Despite the higher concentration of barley, earthworms did not grow faster on this material compared with meadow fescue or lucerne.

Table 4. Mass gain (mg l.m.) of juvenile *A. caliginosa* per g d.m. plant material

Particle size (mm)	Materials						
	Lucerne		Meadow fescue		Barley		
	root	shoot	root	shoot	root	straw	shoot
10.0	—	—	—	—	74 (39)	—	84 (48)
< 1.0	106 (76)	126 (106)	53 (17)	182 (152)	—	—	—
0.2—1.0	—	—	—	—	203 (185)	116 (98)	—
< 0.2	—	—	—	—	218 (200)	224 (206)	—

Note: Mass gain corrected for growth in unamended soil within parentheses.

3.1.1. Lucerne and meadow fescue

Four out of five earthworms added to the soil-lucerne mixtures, both shoots and roots, died within a few days. New earthworms were added when the mixtures had aged for 14 days and all survived.

Fig. 1. Growth (mean mass ± S.E.) of *A. caliginosa* fed (a) soil mixed with 1 g of lucerne or meadow fescue, particle size < 1.0 mm, (b) soil mixed with 1 g barley shoots, particle size 10 mm, or 2 g barley straw, particle sizes 0.2 to 1.0 mm or < 0.2 mm, (c) soil or soil mixed with 1 g barley roots, particle size 10 mm, or 2 g barley roots, particle sizes 0.2 to 1.0 mm or < 0.2 mm.

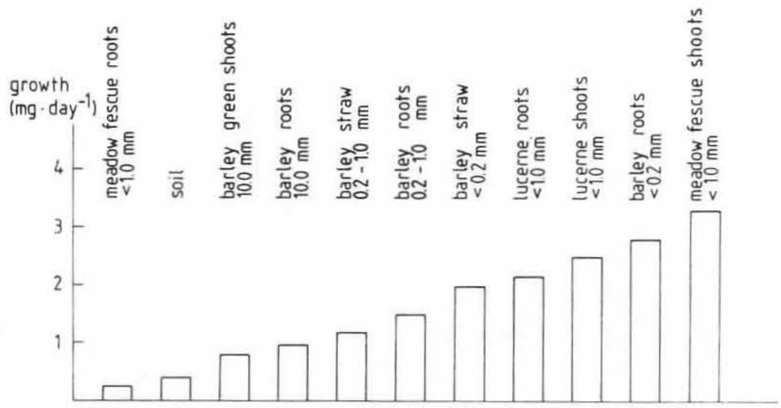


Fig. 2. Growth rate during the first 43 days (mg day^{-1}) of *A. caliginosa* fed soil mixed with different plant materials.

After eight weeks, when most worms had reached their maximum mass, earthworms fed on lucerne roots or shoots weighed about four times more ($p < 0.001$) than those fed on meadow fescue roots (Fig. 1a). Mean mass of earthworms in soil mixed with ground fescue roots was not significantly different from that in unamended soil (Fig. 1c) at this time. Meadow fescue shoots produced significantly higher ($p < 0.05$) masses than lucerne. The treatments resulted in increasing earthworm mass in the order: soil or meadow fescue roots < lucerne roots and shoots < meadow fescue shoots.

A high growth rate during a period is not necessarily correlated to a high final mass. Taking this into consideration growth rates were calculated for two separate periods chosen from the part of the growth curves in Fig. 1a with the steepest slope. During the first period (days 15—21) soil devoid of plant material and meadow fescue roots produced a lower ($p < 0.001$) growth rate than the other materials. During the second period (days 29—43), growth rates on different materials varied in the order listed above.

3.1.2. Barley

Differences in earthworm masses were measured in unamended soil or soil mixed with barley (Table 5). Table 5 should be compared to Fig. 1. Increased particle size of barley straw and roots resulted in lower masses. In this experiment, differences between treat-

Table 5. Mean mass (mg) of earthworms on different days, in unamended soil or soil mixed various barley materials

Day	Particle size (mm)						
	< 0.2 Barley roots	< 0.2 Barley straw	0.2— 1.0 Barley roots	0.2—1.0 Barley straw	10.0 Barley shoots	10.0 Barley roots	Soil
1	22 a	22 a	22 a	22 a	22 a	22 a	22 a
8	34 a	30 ab	30 ab	30 ab	26 b	29 ab	28 ab
22	67 a	57 ab	54 ab	51 ab	46 bc	40 bc	32 c
35	108 a	85 b	71 bc	65 bc	53 cd	57 cd	38 d
51	177 a	130 b	107 b	76 c	73 c	73 c	43 d
66	256 a	175 b	154 bc	107 cd	93 de	76 de	46 e
97	430 a	338 b	321 b	167 c	97 cd	86 d	52 d
127	458 a	470 a	427 a	253 b	106 c	96 c	57 c
158	386 a	436 a	337 a	188 b	103 bc	96 bc	58 c

Note: Standard errors were within 15% of the mean. Means in the same row followed by the same letter are not significantly different ($p < 0.01$).

ments were distinct after seven weeks. Earthworms fed on barley roots < 0.2 mm were heavier ($p < 0.001$) than earthworms on the other materials. Masses in barley straw < 0.2 mm and barley roots 0.2—1.0 mm were higher ($p < 0.01$) than in the remaining materials, and were lowest ($p < 0.01$) in unamended soil.

In experiment II, growth rates were calculated for two separate periods as in the previous experiment. In this case days 35—51 and days 66—97 were compared and statistical results are reported (Table 6). Barley roots 10.0 mm and barley shoots 10.0 mm induced lower growth rate during the second period than during the first, probably because of the lower amount added at the start and they are therefore excluded from Table 6 during period 2.

During the first period the materials produced increasing ($p < 0.01$) earthworm growth rates in the order:

soil barley straw 0.2—1.0 mm barley roots 10.0 mm green barley shoots 10.0 mm	<	barley roots 0.2—1.0 mm barley straw < 0.2 mm	<	barley roots < 0.2 mm

During the second period the order was:

soil	<	barley straw 0.2—1.0 mm	<	barley roots 0.2—1.0 mm barley roots < 0.2 mm barley straw < 0.2 mm

The range of earthworm growth rates was positively correlated to the range of earthworm masses at the beginning of each time period ($r = 0.85$ for time period 1 and $r = 0.72$ or time period 2).

3.2. Toxicity of nitrate and nitrite

In experiment III 900 ppm NO_3^-—N and 300 ppm NO_2^-—N were highly toxic to the earthworms, most of which died within a week. When they were replaced, the new worms also died. No toxic effect was noted by 9 ppm NO_3^-—N or 3 ppm NO_2^-—N.

Fig. 3 shows growth of surviving earthworms in experiment IV. Within five weeks all worms had died in 225 ppm NO_2^-—N and two had died in 110 ppm NO_2^-—N. To enter aestivation seems to be a way for the worms to avoid toxic compounds in the soil. Aestivation was disturbed once a week and worms that were unable to burrow, died on the soil surface.

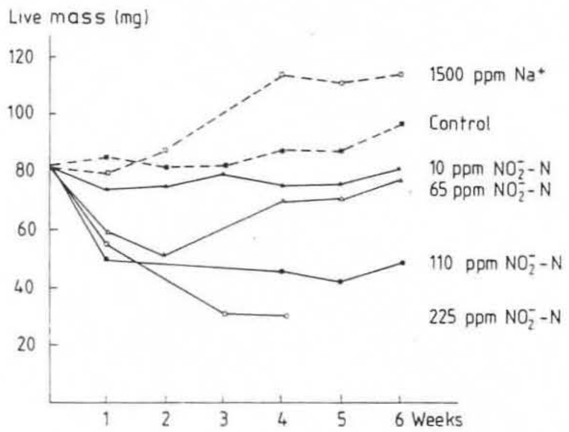


Fig. 3. Mean mass (mg) of *A. caliginosa* in soil mixed with Na_2HPO_4 or $NaNO_2$. Standard errors were within 15% of the mean.

Table 6. Means ± S.E. of earthworm growth rates (mg day^{-1}) for two time periods, and levels of significance for differences in earthworm growth rate in soil mixed with different plant materials

Material and particle size (mm)		Time period	Barley green shoots 10.0	Barley straw < 0.2	Barley straw 0.2—1.0	Barley roots < 0.2	Barley roots 0.2—1.0	Barley roots 10.0	Unamended soil
Barley green shoots	10.0	1	0.9 ± 0.2						
Barley straw	< 0.2	1	**	2.9 ± 0.2					
		2		5.3 ± 0.6					
	0.2—1.0	1	n.s.	***	0.6 ± 0.3				
		2		**	2.3 ± 0.3				
Barley roots	< 0.2	1	***	**	***	4.5 ± 0.3			
		2		n.s.	**	5.1 ± 0.7			
	0.2—1.0	1	*	n.s.	**	***	2.3 ± 0.2		
		2		n.s.	**	n.s.	5.4 ± 0.5		
	10.0	1	n.s.	***	n.s.	***	***	1.0 ± 0.2	
Unamended soil		1	n.s.	***	n.s.	***	***	n.s.	0.3 ± 0.1
		2		***	***	***	***		0.2 ± 0.1

Note: Time period 1 = day 35 to 51, and time period 2 = day 66 to 97. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, n.s. = not significant.

Growth of worms in soil with the three highest NO_2^-—N concentrations was strongly reduced and aestivation was common during the first weeks. Growth in 10 ppm NO_2^-—N was only slightly inferior to that in the control. After three weeks, growth of earthworms in 1,500 ppm Na^+ exceeded that in the control.

3.3. Nitrate, nitrite and ammonium concentration in the soil-lucerne mixture

Nitrate, nitrite and ammonium concentrations in the soil-lucerne mixture never exceeded 38, 10 and 10 ppm respectively.

3.4. Consumption in the field

Plant residues in the top soil of the lucerne fields consisted mainly of lucerne roots and barley straw residues from the previous crop in 1979. In early spring 70 g m^{-2} litter was present on the soil surface (PETTERSSON, pers. com.). One month after rotary cultivation 350 g m^{-2} organic material was found in the soil (HANSSON 1983).

The field population of *A. caliginosa* increased (7.2 $\pm$ 3.2 g m^{-2}) between spring and autumn. This species constituted nearly 90% of the earthworm biomass. Juveniles constituted numerically 76% of the *A. caliginosa* population on 12 May. Fig. 4 shows the estimated amount of plant material needed for net population growth and the amount actually available in the field. One gram of lucerne roots was calculated to increase net live earthworm mass by 76 mg. The corresponding figure for lucerne shoots was 106 mg (Table 4). Mortality and cocoon production in the field were not included in the calculations.

4. Discussion

Particle size had a strong influence on growth. When particle size of a plant material was lowered by a factor of 5, the growth rate doubled. Smaller particles probably enable easier digestion and increase the amount of microorganisms that provide a suitable nu-

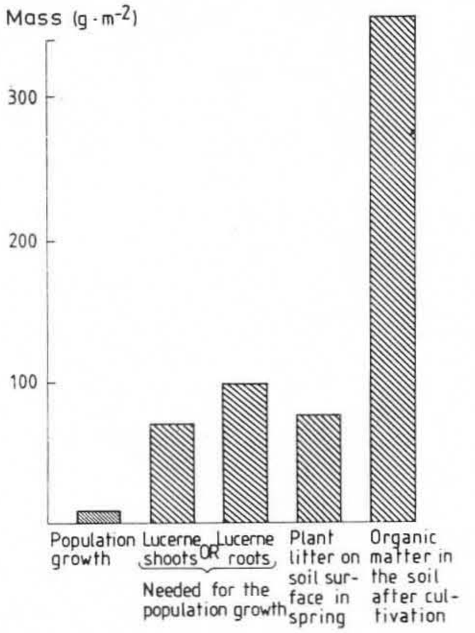


Fig. 4. Growth of *A. caliginosa* population (live mass) from May to September 1981 in a lucerne field, the amount of lucerne (dry mass) theoretically needed for that growth and the amount of lucerne (dry mass) available in the field during the spring and early summer.

trient source (COOKE & LUXTON 1980; NEUHAUSER *et al.* 1980). A similar relationship between particle size and growth of *Eisenia foetida* SAV. was demonstrated by NEUHAUSER *et al.* (1980); growth rate increased when particle size of ground horse manure was decreased from 1.0 to 0.3 mm^2. Fine roots and the small-particle fraction of residues remaining after the harvest of grain crops are thus a more important food source for earthworms than straw, at least during the first year after cultivation.

As the worms were larger at the beginning of the second period growth rates in all ground material were higher during this period than during the first. Large worms gained mass faster than did the small. Barley materials could be divided into three groups producing different earthworm growth rates. Each material produced a comparatively higher growth rate during the second period than during the first, which demonstrates the importance of decomposition of the organic matter when it serves as food for *A. caliginosa*.

In laboratory experiments ABBOTT & PARKER (1981) found that earthworms lost mass on a nitrogen-poor diet. Poor growth on meadow fescue roots might thus be expected because they are low in protein and contain a large proportion of crude fiber (Table 1). Yet barley roots have about the same proportions of crude protein and crude fiber but earthworm growth on barley roots 0.2 to 1.0 mm was eleven times better than on fescue roots < 1.0 mm. Thus, growth rate was affected by something other than crude protein or crude fiber content. The extremely poor growth of earthworms on meadow fescue roots remains unexplained. It is possible that fescue roots contain some compound which retards earthworm growth.

Lucerne roots contained the largest proportion of crude fiber (34%) of all materials tested, while lucerne shoots had only about half that amount (19%). These materials had similar amounts of crude protein, but despite the large difference in crude fiber content, earthworm mass gain on shoots was only slightly higher than on roots. Lucerne shoots have slightly more protein and less crude fiber than fescue shoots, yet fescue shoots produced about 45% higher mass than did lucerne. Although barley roots and straw 0.2 to 1.0 mm contained about the same amount of protein and crude fiber, earthworm mass gain was superior on roots. Thus, no simple relationship between protein, crude fiber and earthworm growth could be established.

Lucerne in early stages of decomposition is probably not a suitable food for earthworms, since toxic substances are either present in the plant or are created by microorganisms in early decomposition stages. Since lucerne is rich in nitrogen, it is possible that a nitrogen compound is formed, in poisonous concentrations, during the first days of decomposition. Neither nitrate nor nitrite in the lucerne/soil mixture seemed to have been the substance responsible for the toxic effects on *A. caliginosa*. However, it is possible that the peak concentrations were overlooked. As the ammonium concentration was less than 10 ppm and CURRY (1976) found very low mortality from 0.1%, ammonium was excluded from further investigation.

Earthworms would need all the litter present on the soil surface in spring, or 20 to 25% of the total amount of plant residues in the soil after cultivation, to support a net biomass increase from 25.8 g m^{-2} in May to 33.0 g m^{-2} in September, i.e. 7.2 g m^{-2} l.m. (Fig. 4). The figures are based on consumption of lucerne roots or shoots. Since mortality and reproduction were disregarded in the field and the materials in the experiment were ground, the amount of plant litter required to sustain this growth in the field population is probably highly underestimated.

Other errors may arise when data from laboratory experiments are converted to field conditions. Besides food supply, earthworm growth is also influenced by temperature and soil humidity. In this study the temperature used (15 °C) agreed well with the daily mean soil temperature at a depth of 15 cm (14 °C) in the field site during the period from 12 May to 15 September, 1981 (unpublished data). Due to sufficient moisture (30%) in the experimental soil no earthworms went into aestivation until the food was almost totally consumed.

In the experiments, growth was calculated only for juvenile earthworms whereas a field population consists of both adults and juveniles of different sizes and ages. On 12 May juveniles constituted the main part of the *A. caliginosa* population in the lucerne field. Hence the net biomass increase from spring to autumn was mainly caused by growth of juvenile worms.

These consumption data can be compared with field data obtained by ANDERSEN (1983). He estimated that a biomass of 23.6 g l.m. *A. caliginosa* per m^2, with an estimated production of 36.6 to 51.2 g l.m. m^{-2} y^{-1}, required a consumption of 295 g d.m. of barley, i.e., 1 g residue per 0.12 to 0.18 g live mass production. This is similar to our estimates of based on earthworm growth on barley straw 0.2 to 1.0 mm or meadow fescue or lucerne shoots < 1.0 mm. ANDERSEN (1983) estimated that earthworms consumed up to 30% if the organic matter in the soil, which is well in accordance with our observations. SYERS & SPRINGETT (1983) emphasized that mineral nutrient requirements of earthworms are relatively high compared to their energy requirement. They assumed an increase in earthworm biomass of 0.8 kg ha^{-1} day^{-1} over 140 days. Based on ingestion rates and with the assumption that plant litter with known nutrient content was the only food source, they estimated that earthworms theoretically required 1 g plant litter per 0.01 g live mass production. It was assumed that 17% of the ingested N had been transferred to earthworm tissue after 140 days. These findings indicate that earthworms are more important in the decomposition process in arable soils than previous estimates based on respiration data have suggested (BARLEY 1964). When earthworms are present they contribute significantly to organic matter turn-over and this must be seriously considered when describing field situations in models and budgets.

5. Acknowledgements

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7. References

ABBOTT, I., & C. A. PARKER, 1981. Interactions between earthworms and their soil environment. Soil Biol. Biochem. **13**, 191—197.

ANDERSEN, N. C., 1983. Nitrogen turnover by earthworms in arable plots treated with farmyard manure and slurry. In: SATCHELL, J. E. (ed.), Earthworm ecology from Darwin to vermiculture. Chapman and Hall. London and New York, pp. 139—150.

Anonymous, 1966. Kungliga lantbruksstyrelsens Kungörelse, Nr. 15, 40—43.

BARLEY, K. P., 1964. Earthworms and the decay of plant litter and dung — a review. Proc. Aust. Soc. Anim. Prod. **5**, 236—240.

BARNES, B. T., & F. B. ELLIS, 1979. Effects of different methods of cultivation and direct drilling and disposal of straw residues, on populations of earthworms. J. Soil Sci. **30**, 669—679.

COOKE, A., & M. LUXTON, 1980. Effect of microbes on food selection by *Lumbricus terrestris*. Rev. Ecol. Biol. Sol **17**, 365—370.

CURRY, J. P., 1976. Some effects of animal manures on earthworms in grassland. Pedobiologia **16**, 425—438.

EDWARDS, C. A., & J. R. LOFTY, 1978. The influence of arthropods and earthworms upon root growth of direct drilled cereals. J. Appl. Ecol. **15**, 789—795.

GINE, M. F., H. BERGAMIN FILHO, E. A. G. ZAGATTO & B. F. REIS, 1980. Simultaneous determination of nitrate and nitrite by flow injection analysis. Anal. Chim. Acta **114**, 191—197.

GRAFF, O., 1971. Stickstoff, Phosphor und Kalium in der Regenwurmlosung auf der Wiesenversuchsfläche des Sollingprojektes. IV. Colloq. Pedobiologiae Ann. Zool. Ecol. Anim. Hors Série, pp. 503—511.

HANSSON, A.-C., 1983. Input of organic matter and nitrogen to an arable soil through root production. In: BÖHM, W., L. KUTSCHERA & E. LICHTENEGGER (eds.), Wurzelökologie und ihre Nutzanwendung. Verlag Gumpenstein. Irdning, pp. 757—760.

— & E. STEEN, 1984. Methods of calculating root production and nitrogen uptake in an annual crop. Swedish J. agric. Res. **14**, 191—200.

HOOGERKAMP, M., H. ROGAAR & H. J. P. EIJSACKERS, 1983. Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: SATCHELL J. E. (ed.) Earthworm ecology from Darwin to vermiculture. Chapman and Hall. London and New York pp. 85—104.
LOFS-HOLMIN, A., 1983a. Earthworm population dynamics in different agricultural rotations. In: SATCHELL, J. E. (ed.), Earthworm ecology from Darwin to vermiculture. Chapman and Hall. London and New York, pp. 151—160.
LOFS-HOLMIN, A., 1983b. Influence of agricultural practices on earthworms (Lumbricidae). Acta Agric. Scand. **33**, 225—234.
NEUHAUSER, E. F., D. L. KAPLAN, M. R. MALECKI & R. HARTENSTEIN, 1980. Materials supporting weight gain by the earthworm *Eisenia foetida* in waste conversion systems. Agricultural Wastes **2**, 43—60.
PIEARCE, T. G., 1978. Gut contents of some lumbricid earthworms. Pedobiologia **18**, 153—157.
RAW, F., 1959. Estimating earthworm populations by using formalin. Nature (London) **184**, 1661.
RUZICKA, J., & E. H. HANSEN, 1975. Flow injection analysis. Part I. A new concept of fast continuous flow analysis. Anal. Chim. Acta, **78**, 145—157.
STEEN, E., P.-E. JANSSON & J. PERSSON, 1984. Experimental site of the "Ecology of Arable Land" project. Acta Agric. Scand. **34**, 153—166.
STOUT, J. D., 1983. Organic matter turnover by earthworms. In: SATCHELL, J. E. (ed.), Earthworm ecology from Darwin to vermiculture. Chapman & Hall, London and New York, pp. 35—48.
— & K. M. GOH, 1980. The use of radiocarbon to measure the effects of earthworms on soil development. Radiocarbon **22**, 892—896.
SYERS, J. K., & J. A. SRINGETT, 1983. Earthworm ecology in grassland soils. In: SATCHELL, J. E. (ed.), Earthworm ecology from Darwin to vermiculture. Chapman and Hall. London and New York, pp. 67—83.

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Synopsis: *Original scientific paper*

BOSTRÖM, U., & A. LOFS-HOLMIN, 1986. Growth of earthworms *(Allolobophora caliginosa)* fed shoots and roots of barley, meadow fescue and lucerne. Studies in relation to particle size, protein, crude fiber content and toxicity. Pedobiologia **29**, 1—12.

Juvenile earthworms showed extremely different growth rates when fed different plant materials. Particle size was a most important factor, but protein and crude fiber content could not be correlated to growth rate. Earthworms gained mass well on barley roots but not in soil with meadow fescue roots even though both root materials were similar in protein, crude fiber content and particle size. The reason for this remains unexplained.

Fresh mixtures of soil and lucerne were toxic to the earthworms, but toxicity diminished after ageing and then the mixtures promoted good growth. Inorganic compounds such as nitrate, nitrite or ammonium were ruled out as being the cause of toxicity.

For a net production of 7.2 g m^{-2} l.m., a lucerne field population of earthworms was estimated to consume at least 20 to 25% of the total amount of plant residues in the soil or all plant litter present on the soil surface in spring.

Key Words: earthworms, growth, lucerne, meadow fescue, barley, toxicity, consumption.